

LIGHT INTERCEPTION AND USE EFFICIENCY DIFFER WITH MAIZE PLANT DENSITY IN MAIZE-PEANUT INTERCROPPING

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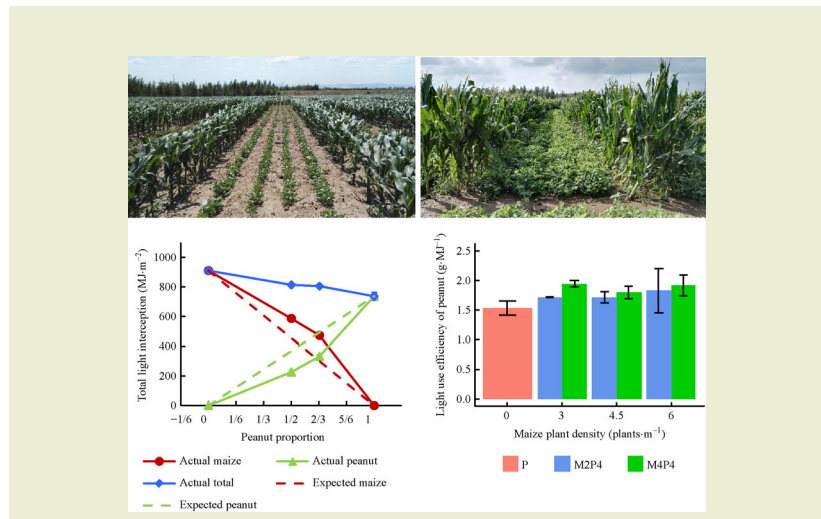
KEYWORDS

dryland agriculture, light interception, light use efficiency, maize-peanut intercropping, semiarid

HIGHLIGHTS

- Intercropping intercepted more light than sole peanut but less than sole maize.
- Maize light use efficiency (LUE) increased with plant density in the intercropping.
- Intercropping did not affect LUE of maize but increased peanut LUE.

GRAPHICAL ABSTRACT



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ABSTRACT

Intercropping increases crop yields by optimizing light interception and/or use efficiency. Although intercropping combinations and metrics have been reported, the effects of plant density on light use are not well documented. Here, we examined the light interception and use efficiency in maize-peanut intercropping with different maize plant densities in two row configurations in semiarid dryland agriculture over a two-year period. The field experiment comprised four cropping systems, i.e., monocropped maize, monocropped peanut, maize-peanut intercropping with two rows of maize and four rows of peanut, intercropping with four rows of maize and four rows of peanut, and three maize plant densities (3.0, 4.5 and 6.0 plants m⁻¹ row) in both monocropped and intercropping maize. The mean total light interception in intercropping across years and densities was 779 MJ·m⁻², 5.5% higher than in monocropped peanut (737 MJ·m⁻²) and 7.6% lower than in monocropped maize

(843 MJ·m⁻²). Increasing maize density increased light interception in monocropped maize but did not affect the total light interception in the intercrops. Across years the LUE of maize was 2.9 g·MJ⁻¹ and was not affected by cropping system but increased with maize plant density. The LUE of peanut was enhanced in intercropping, especially in a wetter year. The yield advantage of maize-peanut intercropping resulted mainly from the LUE of peanut. These results will help to optimize agronomic management and system design and provide evidence for system level light use efficiency in intercropping.

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1 INTRODUCTION

Intercropping, growing two or more crop species in the same field, has been proposed to help in both higher productivity and environmental sustainability^[1]. Monocropping in China has delivered production increases over recent decades but this has come at the cost of high resource inputs, including fertilizers and irrigation^[2]. The most remarkable advantage of intercropping is providing yield advantage over monocropping^[3] by increasing resource capture and/or use efficiencies including light, nitrogen and water^[4–6]. Also, intercropping systems can reduce soil erosion, plant diseases and weeds and increase soil fertility^[7–9]. In semiarid regions, drought affects the production of rainfed maize^[10] and wind erosion occurs in monocropped peanut following soil disturbance at harvest. Integrating maize and peanut in strip intercropping is a practical option for farmers.

Light interception and light use efficiency (LUE) of crops directly determine dry matter accumulation and yield formation, depending on canopy traits such as the distribution and photosynthetic capacity of the leaves^[11–15]. Higher light interception or a higher LUE can result in greater productivity. Numerous studies reported that yield advantage in intercropping was mainly due to greater light interception and use efficiency. There are different types of intercropping. Relay intercropping is the growth of different species with partial temporal overlap during the growing period. Strip intercropping is growth of two or more crop species in alternate strips. Intercropping with early- and late-developing species in combination such as wheat and cotton with different canopy development stages^[4] can increase the period of soil cover to enable more light interception. Tall and short species in combination, such as maize-peanut intercropping systems^[16] can increase light interception due to the increased soil cover. Also, the combination of shorter C₃ and taller C₄ species in intercropping can increase the LUE as C₄ species have higher saturation points than C₃ species^[17]. The taller C₄ species are more likely to benefit from a higher light intensity environment in intercropping than in monocropping, and the companion crops are often C₃ species and shorter. Compared with a

monocrop, the shaded C₃ species in intercropping can have a higher LUE at lower light intensity^[18]. The advantage of strip intercropping over other intercropping systems like mixed intercropping or row intercropping is the relative convenience of mechanized operations. In contrast to relay intercropping, strip intercropping benefits from spatial complementarity but with no temporal advantage. Plant density is one of the most practical ways to change canopy traits and affect the interaction between crop species. However, it remains unclear how light interception and use efficiency respond to the plant density of dominant species in monocropping and intercropping.

Plant density is an important attribute that can be managed to alter competition and interactions between plants to influence crop growth. By increasing the plant density of the dominant crop the allocation of dry matter to the leaves increases^[16], resulting in a linear increase in leaf area index (LAI)^[19]. The competitive ability of a crop may be enhanced when the dry matter allocation to organs changes with plant density^[20,21]. Increased LAI and competitive ability help to intercept more light. However, when increasing the plant density of a taller crop the LAI of a shaded species decreases^[22,23], leading to a negative effect on light interception. Thus, we hypothesized a trade-off between light interception of two crops with increased density of the dominant species. The LUE of a crop is genetically stable^[15] but is closely related to environmental factors that affect photosynthesis such as light and water. LUE increases in a crop going from direct to diffuse light^[24] and differs among species and with water supply, leaf nitrogen content and temperature^[25]. Canopy structure and light distribution vary with plant density in both monocropping and intercropping^[26]. When maize density is too high the high LAI reduces the light penetration to the lower canopy^[27], accelerating the senescence of the lower leaves^[28] and reducing the LUE^[29]. It is therefore necessary to explore whether plant density in intercropping is a factor affecting the LUE.

Maize-peanut intercropping might be a way of mitigating drought risk in monocropped maize in semiarid areas. Moreover, the soil erosion after the harvest of monocropped peanut

may also be relieved by the maize stubble remaining in intercropping. Strip width is an important factor influencing light interception in intercropping^[30]. However, it not clear how strip width affects the density effect on light interception in intercropping. Here, we have conducted a maize-peanut experiment with different strip widths in semiarid conditions to quantify (1) the plant density effects on light interception in monocropped maize and intercropping systems and (2) the light interception and use efficiency of each species in maize-peanut intercropping in response to maize plant density.

2 MATERIALS AND METHODS

2.1 Experimental design

The experiment was conducted in 2016 and 2017 at Fuxin, Liaoning Province, north-east China (42°09'02" N, 121°43'48" E). From 1965 to 2015, the average precipitation during the growing season (May to September) was 531 mm with a standard deviation of 134 mm. The climate is classified as Dwa, representing cold, dry winters and hot summers according to the Köppen-Geiger classification^[31]. The active cumulative temperature above 10°C is 3414°C with a frost-free period of 175 days. The soil is a sandy Arenosol^[32] with a bulk density of 1.45 g·cm⁻³ averaged over 0–20 cm soil depth. In the top 20 cm of the soil profile the organic matter content is 14.4 g·kg⁻¹ with total N content of 0.78 g·kg⁻¹, available N of 45.2 mg·kg⁻¹, available P of 17.4 mg·kg⁻¹, and available K of 69.5 mg·kg⁻¹. Total N was determined by the Kjeldahl method, available N by the alkaline hydrolysis diffusion method, available P by 0.5 mol·L⁻¹ NaHCO₃ extraction, and available K by ammonium acetate extraction.

Maize hybrid Zhengdan 958 and peanut cv. Baisha1016 were sown and harvested simultaneously. In 2016, sowing was on May 21 and harvest on September 30, and in 2017, the corresponding dates were May 24 and September 30. Each plot was 96 m² (8 m × 12 m) with north–south row orientation. No irrigation was applied. Fertilizer was applied to maize and peanut in the planting row according to farmers, practice with all systems receiving the same amounts, namely 112 kg N, 49 kg P, and 93 kg K ha⁻¹.

The experiment was laid out in a complete randomized block design. There were 10 treatments comprising four cropping systems and three maize plant densities. There were three replicates of each treatment. The four cropping systems were monocropped maize, monocropped peanut, intercropping with four rows of maize alternating with four rows of peanut (M4P4), and intercropping with two rows of maize alternating with four

rows of peanut (M2P4). The three maize densities were achieved by adjusting plant distance in the rows to 33, 22 and 17 cm to obtain plant densities of 3, 4.5 and 6 plants m⁻¹ row. Distance between rows was 50 cm within and between maize and peanut in all treatments^[33]. Taking into account the land use proportion in the intercropping, the homogeneous maize plant densities per unit ground area for the intercropping were 6, 9 and 12 plants m⁻² in monocropping, 3, 4.5 and 6 plants m⁻² in M4P4, and 2, 3 and 4 plants m⁻² in M2P4. Peanut plant density was 12 plants m⁻¹ row in all treatments with a land use proportion of 0.5 for both maize and peanut in M4P4, and 0.33 for maize and 0.67 for peanut in M2P4.

2.2 Measurements

LAI and plant height of both maize and peanut were determined four times in both 2016 (June 22, August 23 and September 25) and 2017 (July 6, August 9, September 6 and September 29). With intercropped treatments, the first row (or border row) was the first row adjacent to another species, and the second row (or inner row) was the second row adjacent to another species. Three plants were arbitrarily selected in each plot in monocropped maize, and three plants in intercrops at the first and second row in each plot to determine leaf area and plant height. One-m row was arbitrarily selected for monocropped peanut, and in intercrops at the first and second row in each plot to measure leaf area and plant height.

The length and width (at the widest point) of each leaf were measured. The leaf area of maize was calculated as the product of length, width and the coefficient 0.75. Fifty peanut leaves were selected to determine the ratio (μ) between leaf area and dry matter and the leaf areas of 50 leaves were measured with a leaf area meter. The leaf area of peanut was the product of total dry matter and the ratio μ . The LAI was the leaf area per unit ground area. The plant heights of maize and peanut were recorded with the natural height, i.e., the height from the soil surface to the highest point in the field.

The final dry matter, which was used to compute LUE, was measured at harvest. The dry matter samples were three randomly selected harvested plants from each plot of monocropped maize and one-meter row length in each plot of monocropped peanut. In the intercropping treatments, maize samples were three randomly selected plants from the first and second rows in each plot, and peanut samples were 1 m of randomly selected row in both rows. Plant samples were partitioned into leaves, stems and seeds. The dry mater weight was determined after drying to a constant weight at 85°C for 24 h.

2.3 Data analysis

2.3.1 Leaf area index dynamics

To quantify crop growth, a flexible sigmoid function^[34] was used to determine the dynamics of LAI in each treatment.

$$LAI = LAI_m \left(1 + \frac{t_e - t}{t_e - t_m} \right) \left(\frac{t}{t_e} \right)^{\frac{t_e}{t_e - t_m}} \quad 0 \leq t \leq t_e \quad (1)$$

$$C_m = LAI_m \left(\frac{2t_e - t}{t_e(t_e - t_m)} \right) \left(\frac{t_m}{t_e} \right)^{\frac{t_m}{t_e - t_m}} \quad 0 \leq t \leq t_e \quad (2)$$

where LAI is the value of the crop leaf area index, LAI_m is the maximum value of LAI, t_e is the time at which this maximum LAI_m was reached, C_m is the maximum growth rate of LAI (d^{-1}) and t_m is the time at which this maximum growth rate was reached. These equations were restricted to the time domain $0 < t < t_e$ ^[30]. These equations were used for the measured data of LAI and as input to calculate light interception.

2.3.2 Estimation of light interception

The cumulative light interception of the crop during the growing season was obtained by summing daily light interception which was calculated as the product of daily incoming photosynthetically active radiation (PAR) and the fraction of light intercepted. The daily incoming PAR was calculated based on weather data obtained from a local weather station (Fig. 1). Plant height, leaf area index, strip width, light extinction coefficient and weather data were used as the inputs to a strip structured light interception model^[4,35]. The light extinction coefficients

used in the model were 0.65 (maize^[36]) and 0.85 (peanut^[37]). Together, these six variables (height, LAI and strip width of each species) determined the partitioning and interception of light.

Expected light interception was calculated for each crop species as follows:

$$LI_{\text{expected},j} = LI_{\text{sole},j} \times p \quad (3)$$

where $LI_{\text{expected},j}$ is the expected light interception in intercropping at a plant density of j , $LI_{\text{sole},j}$ is the light interception in monocropped stands at a density of j , and p is the land use proportion.

2.3.3 Light use efficiency

LUE was determined as the ratio of final aboveground biomass to total cumulative light interception during the growing season. The calculations were made with the data from each plot using analysis of variance.

2.3.4 Statistical analysis

Mixed-effect models were used to analyze density and configuration effects on dry matter, light interception, LUE and species-specific metrics. Systems were monocropping and M4P4 and M2P4 intercropping. All statistical analyses were conducted using R (version 3.5.0). Models were fitted using the function *lme* in the R package “nlme”^[38]. The growth of leaf area index was fitted using maximum likelihood estimation using the R function *mle2* in the R package “bbmle”^[39].

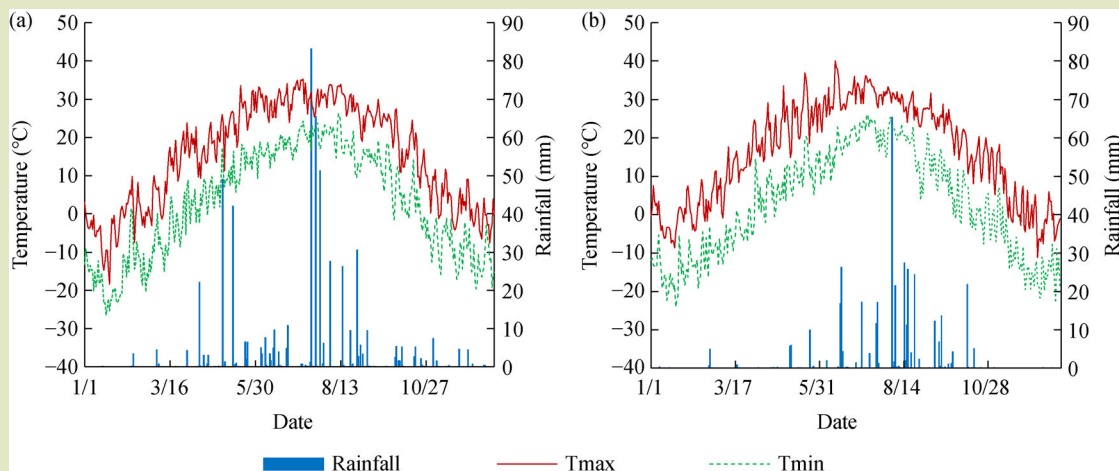


Fig. 1 Daily maximum (Tmax) and minimum (Tmin) temperatures and rainfall in 2016 (a) and 2017 (b) in Fuxin, Liaoning Province. The total annual rainfall was 580 mm in 2016 and 386 mm in 2017.

3 RESULTS

3.1 Plant height

In monocropped maize the plant height increased with increasing maize density ($P < 0.05$). However, plant height was not affected by density when intercropped ($P > 0.05$) (Fig. 2). At 3.0 and 4.5 plants m^{-1} , maize plant height in intercropping was

not significantly different from that of monocropped maize. However, at 6.0 plants m^{-1} , plant height of monocropped maize was greater than that of intercropped maize.

The final plant height of peanut in intercropping decreased with increasing maize density ($P < 0.05$) (Fig. 3). Monocropped peanut was taller than intercropped peanut with high maize density of M4P4 intercropping and had a similar height to intercropped

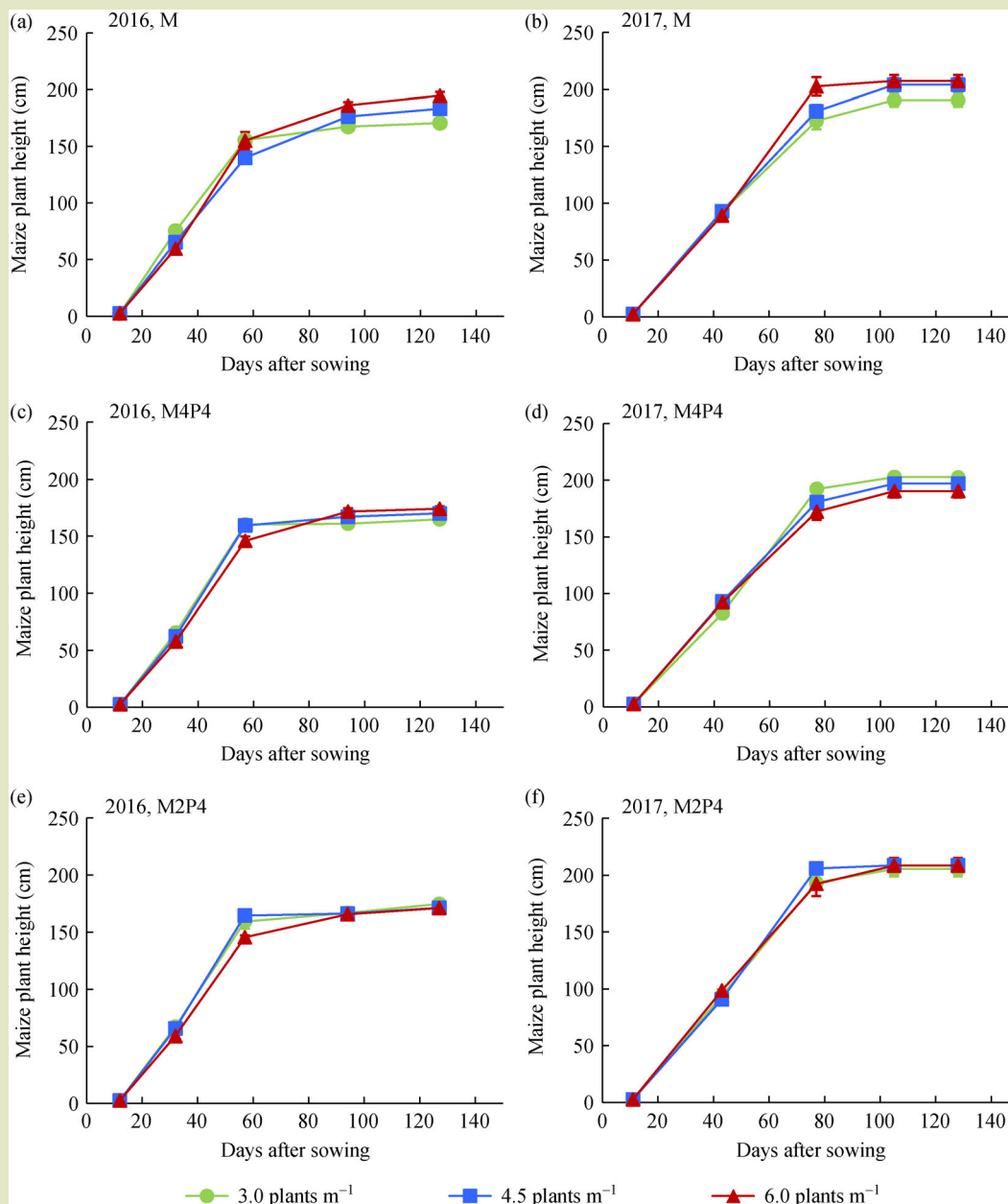


Fig. 2 Plant height of maize in monocropping and intercropping systems at three maize densities. M represents monocropped maize; M4P4 is the intercropping systems of four rows maize with four rows peanut; M2P4 is the intercropping systems of two rows maize with four rows peanut. Error bars are the standard error values.

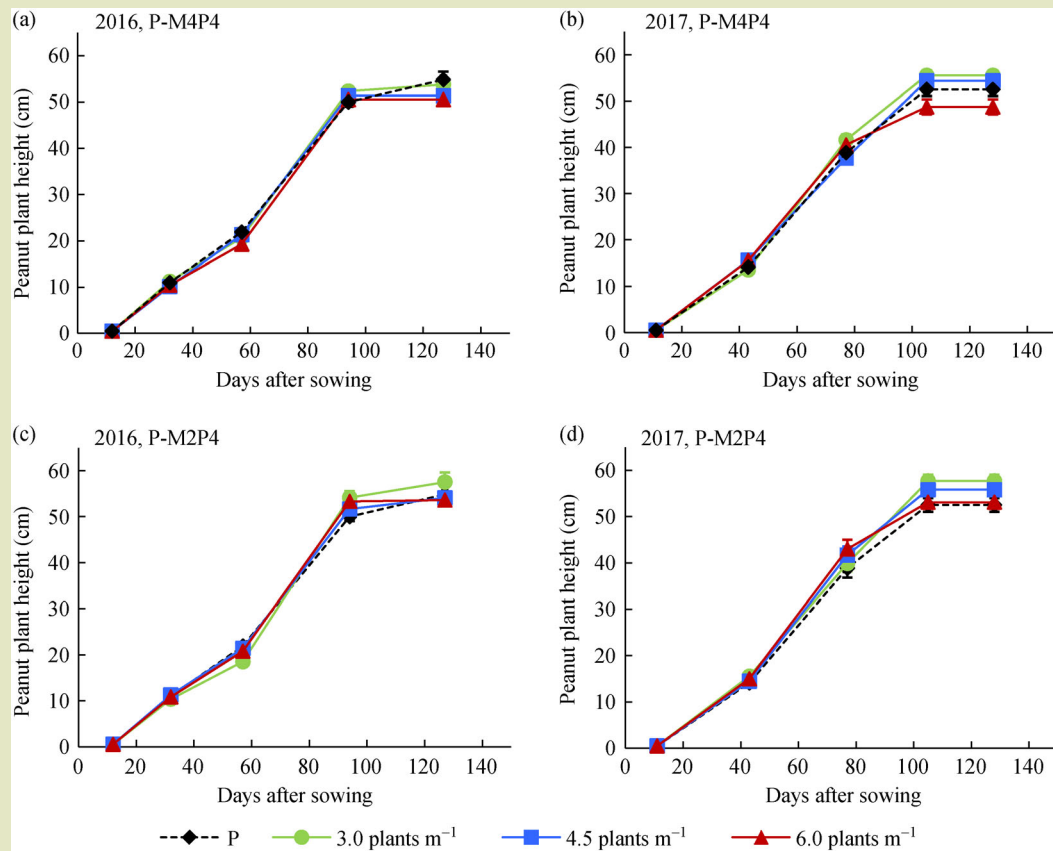


Fig. 3 Plant height of peanut in monocropping and intercropping with three maize densities. P represents the monocropped peanut; M2P4 is the intercropping systems of two rows maize with four rows peanut; M4P4 is the intercropping systems of four rows maize with four rows peanut. Error bars are the standard error values.

peanut with high maize density in M2P4. However, monocropped peanut height was similar to intercropped peanut with high maize density.

3.2 Leaf area index

The leaf area index of maize was highest at six plants m^{-2} and lowest at three plants m^{-2} in both monocrops and intercrops (Fig. 4). The maximum LAI (LAI_m) of maize increased with maize density in both monocropping and intercropping (Table 1). Across years and densities, the LAI_m of maize was 5.51 in monocropped maize, 2.97 in M4P4, and 2.16 in M2P4. Taking into consideration the land use percentages of maize in M4P4 (0.5) and M2P4 (0.3), the LAI_m of intercropped maize was 17.2% and 7.7% higher than that of monocropped maize. The time taken to reach LAI_m (t_e) was not significantly different between density and system but was 7 days earlier in 2016 than in 2017 (Table 1). The maize C_m did not differ between years ($P = 0.082$) at any plant density. However, plant density, cropping

system and their interactions significantly affected maize C_m . Maize C_m was higher at high density than at low density in all cropping systems and was higher in M4P4 than in M2P4. The time taken to reach C_m (t_m) did not differ with density or system but was 22 days later in 2017.

The LAI of peanut decreased with maize plant density in both M4P4 and M2P4 (Fig. 5). The LAI_m of peanut across years was 4.16 in monocropping, 1.44 in M4P4 and 2.00 in M2P4. Taking into account the 50% land use percentage in M4P4 and 67% in M2P4, the LAI_m values of peanut in M4P4 and M2P4 across years were 2.88 and 2.99, i.e., 30.8% and 28.1% lower than in monocropping. The t_e of intercropped peanut was on average 4 days earlier than in monocropped peanut (Table 1). Peanut C_m was significantly affected only by cropping system. Taking into account the land use percentage the intercropped peanut C_m was 59.1% lower than in monocropping. The t_m of intercropped peanut was earlier than that of monocropped peanut but was 6 days later in 2016 than in 2017 (Table 1).

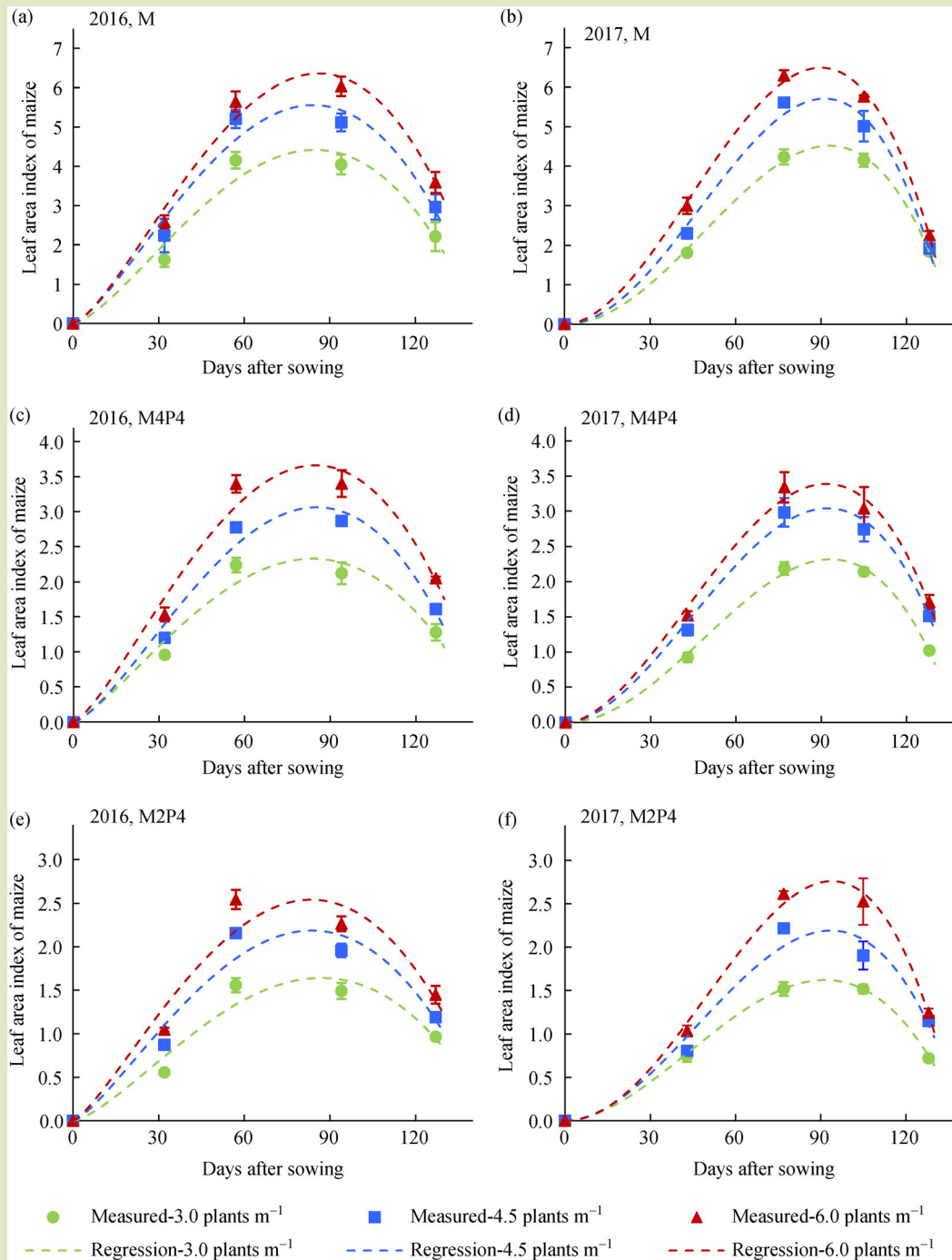


Fig. 4 Leaf area index (LAI) of maize in response to maize densities in monocropping and intercropping systems. M represents monocropped maize; M4P4 is the intercropping systems of four rows maize with four rows peanut; M2P4 is the intercropping systems of two rows maize with four rows peanut. The regression data was calculated by Eq. (1) and Eq. (2). Error bars are the standard error values.

3.3 Light interception

The fraction of light interception of intercropped maize in response to plant density was weaker than that of monocropped

maize (Fig. 6). Across years, with increasing maize density the average fraction of maize light interception during the whole growing season increased by 12.4% (0.75–0.85) in monocropping, 17.6% in M4P4 (0.46–0.54) and 22.0% in M2P4

Table 1 Fitted parameters for the growth of leaf area index (LAI) in maize and peanut in different systems, monocropping (Mono) and two intercropping (M4P4 and M2P4) systems

Year	System	Maize plant density (plants m ⁻¹)	Maize				Peanut			
			LAI _m (m ² ·m ⁻²)	t _e (d)	C _m (m ² ·m ⁻² ·d ⁻¹)	t _m (d)	LAI _m (m ² ·m ⁻²)	t _e (d)	C _m (m ² ·m ⁻² ·d ⁻¹)	t _m (d)
2016	Mono	3.0	4.42 c	84.8 a	0.075 b	27.0 a				
		4.5	5.56 b	84.2 a	0.097 a	24.0 a	4.03	98.5	0.068	60.4
		6.0	6.36 a	86.2 a	0.107 a	25.9 a				
	M4P4	3.0	2.33 c	84.9 a	0.041 c	22.1 a	1.51 a	96.1 a	0.025 a	55.3 a
		4.5	3.06 b	85.3 a	0.052 b	26.9 a	1.38 a	95.5 a	0.023 a	53.6 a
		6.0	3.66 a	84.8 a	0.063 a	23.2 a	1.26 a	95.8 a	0.021 a	53.4 a
	M2P4	3.0	1.64 c	86.9 a	0.027 c	26.9 a	2.11 a	98.0 a	0.034 a	56.6 a
		4.5	2.18 b	83.6 b	0.038 b	21.5 ab	1.94 a	96.0 a	0.031 a	52.7 a
		6.0	2.54 a	83.4 b	0.045 a	19.9 b	1.90 a	97.2 a	0.033 a	59.9 a
2017	Mono	3.0	4.52 c	92.9 a	0.074 c	48.8 a				
		4.5	5.72 b	91.2 ab	0.095 b	47.4 a	4.28	98.4	0.071	59.9
		6.0	6.49 a	89.9 b	0.108 a	43.9 a				
	M4P4	3.0	2.32 b	93.3 a	0.038 b	48.6 a	1.57 a	91.8 a	0.026 a	47.3 a
		4.5	3.04 a	92.3 a	0.048 a	43.7 a	1.53 a	91.7 a	0.025 a	46.4 a
		6.0	3.39 a	91.8 a	0.054 a	42.5 a	1.39 a	91.9 a	0.023 a	46.5 a
	M2P4	3.0	1.62 c	91.6 a	0.027 c	43.3 a	2.19 a	94.1 a	0.036 a	52.3 a
		4.5	2.19 b	93.6 a	0.035 b	46.4 a	1.98 ab	92.2 a	0.033 a	48.8 a
		6.0	2.76 a	94.1 a	0.045 a	49.9 a	1.85 b	92.6 a	0.031 a	50.6 a
Interaction			P value							
Density			0.000	0.346	0.000	0.254	0.086	0.489	0.142	0.903
System			0.000	0.539	0.000	0.545	0.000	0.000	0.000	0.002
Year			0.675	0.000	0.082	0.000	0.246	0.000	0.313	0.001
Density × System			0.0004	0.928	0.001	0.765	–	–	–	–
Density × Year			0.990	0.804	0.733	0.795	0.902	0.948	0.794	0.669
System × Year			0.437	0.181	0.417	0.635	0.634	0.129	0.843	0.402
Density × System × Year			0.546	0.002	0.584	0.033	–	–	–	–

Note: LAI_m is the maximum value of LAI, t_e is the time at which this maximum LAI_m was reached, C_m is the maximum growth rate of LAI (m²·m⁻²·d⁻¹) and t_m is the time at which this maximum growth rate was reached. Means followed by same letter indicate no significantly different between densities in a certain system at α = 0.05 level. M4P4 is intercropping of four rows maize with four rows peanut; M2P4 is intercropping of two rows maize with four rows of peanut.

(0.36–0.45). The fraction of light intercepted by intercropped peanut at flowering (days after sowing from 72 to 102) was 0.95 in monocropping, 0.30 in M4P4 and 0.43 in M2P4. With increasing maize density, the fraction of light intercepted by intercropped peanut decreased.

With increasing maize density the total light interception varied from 787 to 891 MJ·m⁻² in intercropping, 749 to 799 MJ·m⁻² in M4P4 and 754 to 791 MJ·m⁻² in M2P4. The increment of light interception due to density increase was 13.1% in monocropped

maize and 0.6% in intercropping. In M4P4, intercropping intercepted 5.7% more light than monocropped peanut but 7.5% less than monocropped maize. The total light interception of M2P4 was 778 MJ·m⁻² across years and densities, 5.4% higher than that in monocropped peanut and 7.7% lower than in monocropped maize.

The light interception of intercropped maize in M4P4 was 527 MJ·m⁻², 25.1% higher than the expected value across years and densities and 53.0% higher in M2P4 (425 MJ·m⁻²) than

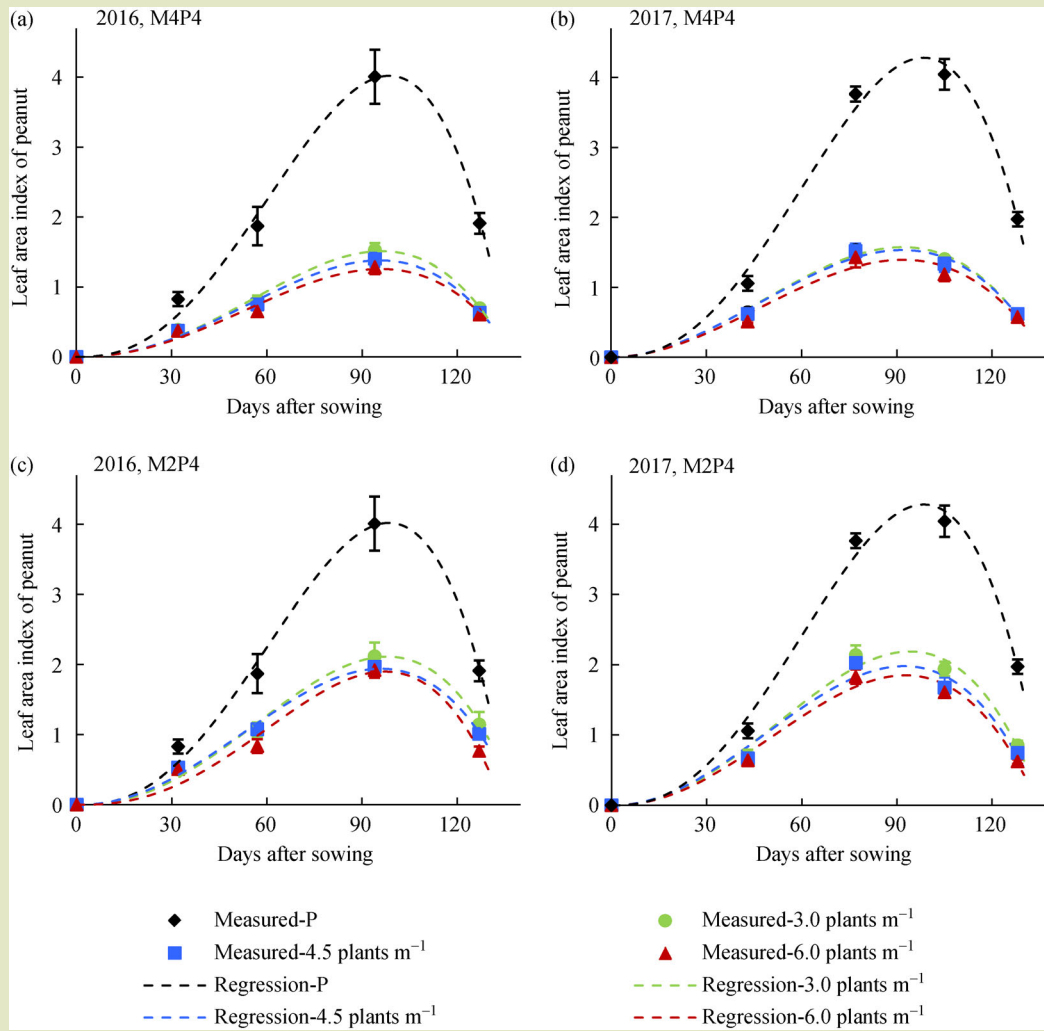


Fig. 5 Leaf area index (LAI) of peanut in response to maize densities in monocropping and intercropping systems. M4P4 represents the intercropping systems of four rows maize with four rows peanut; M2P4 represents the intercropping systems of two rows maize with four rows peanut; P represents monocropped peanut. The regression data were calculated by Eq. (1) and Eq. (2). Error bars are the standard error values.

expected (Fig. 7). In peanut the light interception in the intercrop was 421 MJ·m⁻² in M4P4, 49.0% lower than expected, and 352 MJ·m⁻² in M2P4, 28.7% lower than expected.

3.4 Light use efficiency

The LUE of maize changed with increased density but showed no significant difference between monocropped and intercropped maize at the same maize plant distance (Table 2). With increasing maize plant density from 3.0 to 4.5 plants m⁻¹, maize LUE increased slightly in M2P4 intercropping in 2016 and monocropped maize in 2017 but there was no significant difference with increasing density from 4.5 to 6.0 plants m⁻¹. The LUE of peanut in intercropping was not affected by maize plant

density but was higher in intercropping than in monocropped peanut across years ($P = 0.032$).

4 DISCUSSION

Light interception was higher in maize-peanut intercropping than in monocropped peanut but lower than in monocropped maize. The light interception advantage in intercropping is attributed mainly to temporal and spatial complementarity which increases the soil cover over space and time. In relay intercropping, both crop species benefitted from intercropping in terms of light interception, mainly due to the different growth and development stages prolonging the time of light

interception^[3,4,40]. However, in the intercropping system used here the two crops were grown and harvested simultaneously. Due to its greater height and leaf area index than in peanut, maize was dominant in light interception in the intercropping system. The intercropped maize showed a large advantage of light interception over monocropped maize at the expense of the

understory peanut due to the increased leaf area index and space occupation in the upper canopy. However, peanut grew with shading by maize, leading to less light reaching the peanut canopy and decreased light interception. Thus, the benefit of maize light interception in the intercropping was largely offset by the disadvantage to peanut.

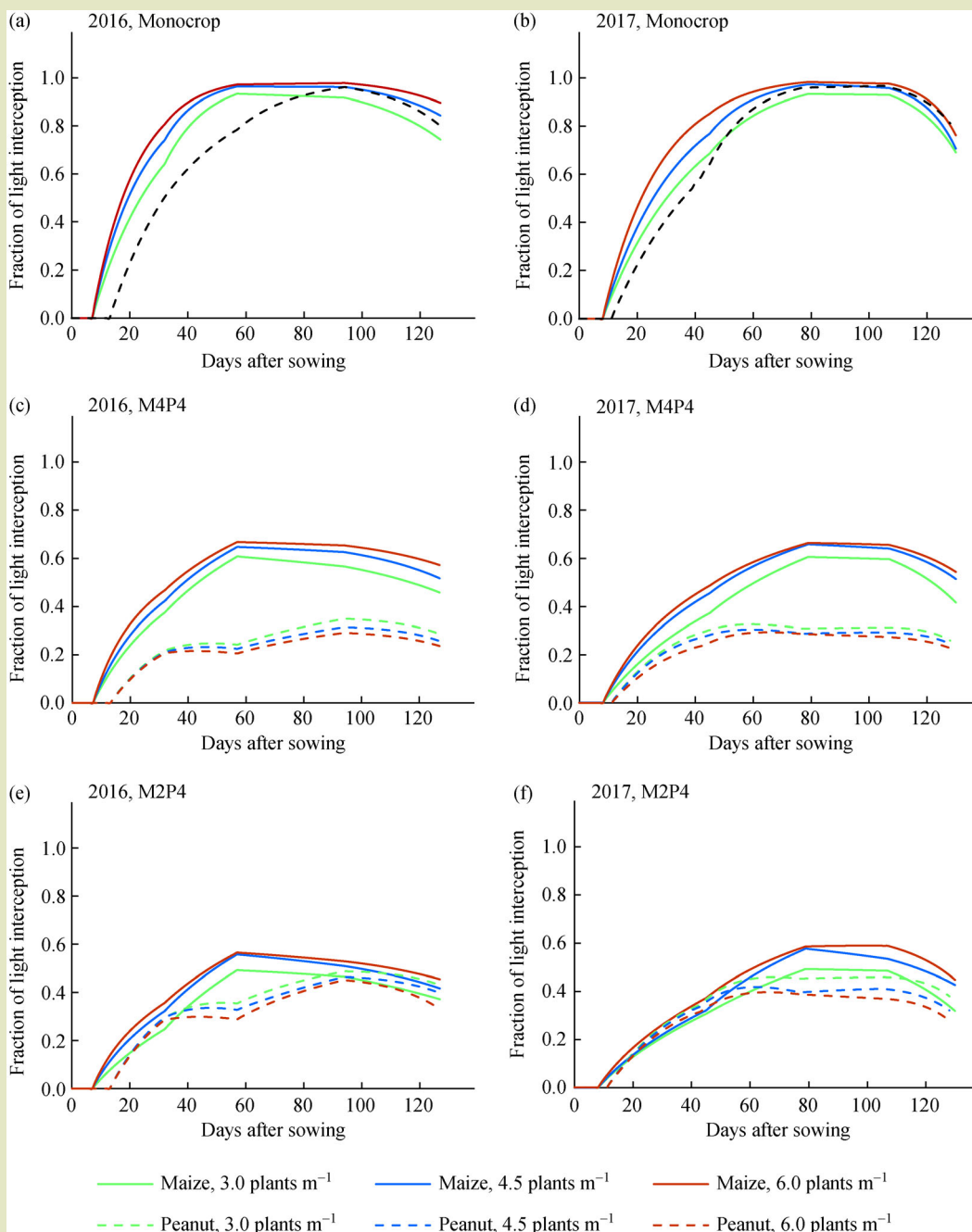


Fig. 6 Fraction of light interception in response to maize density in monocropping and intercropping systems. In the panels (a) and (b), the black dashed line represents the fraction of light interception of monocropped peanut. M4P4 represents the intercropping systems of four rows maize with four rows peanut; M2P4 represents the intercropping systems of two rows maize with four rows peanut.

The total light interception in the intercropping did not change significantly with increasing maize plant density but did increase with increasing density in monocropped maize. This indicates that the optimum plant density for maize in intercropping might be lower than in monocropping, confirming previous conclusions from yield analysis^[33]. Crop light interception was

positively related to leaf area index^[41]. In monocropped maize, the light interception increased with increasing plant density, mainly due to the increased leaf area index. However, the results show that the leaf area index of intercropped maize increased with increasing maize plant density but decreased marginally in the intercropped peanut. It may be concluded that overall leaf

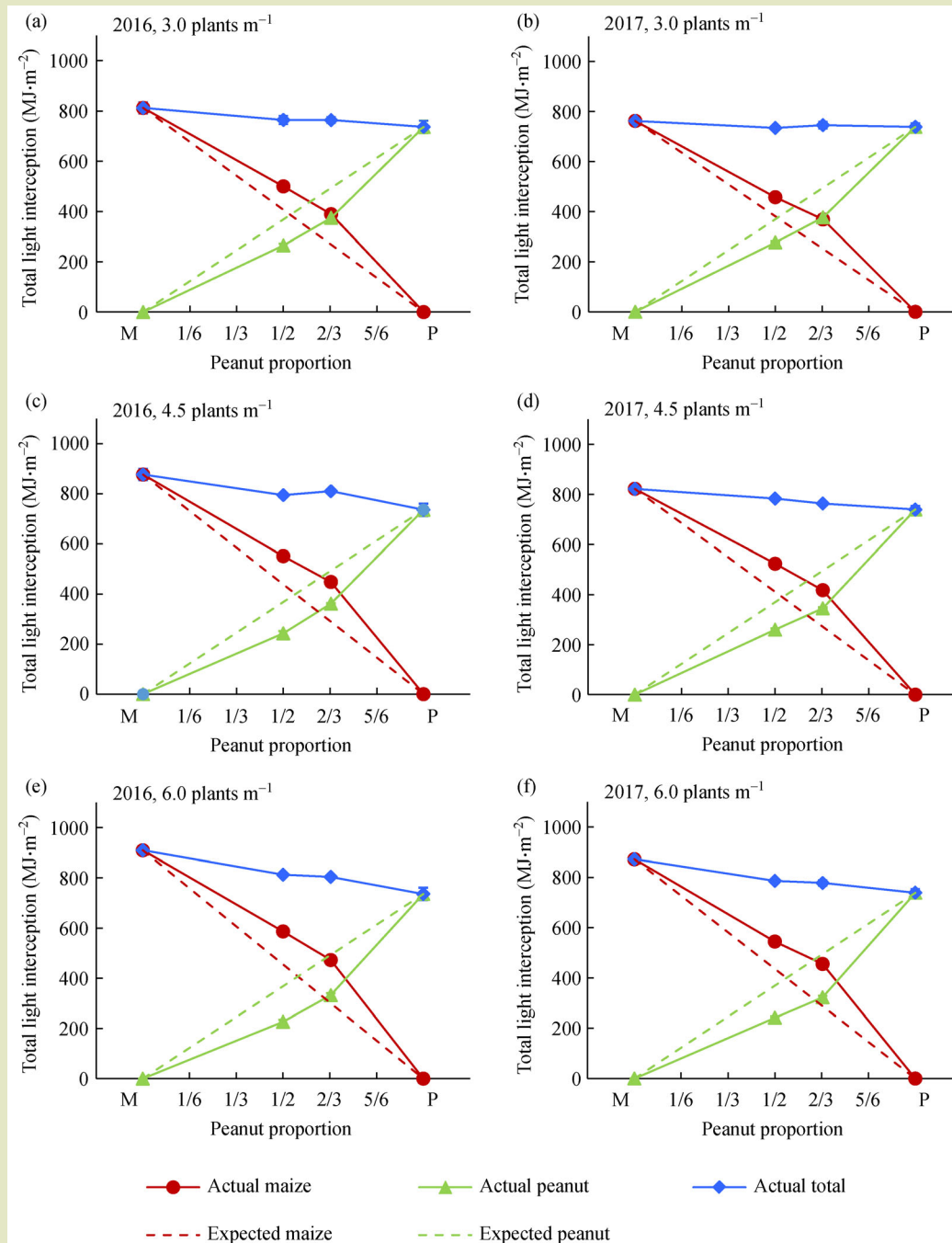


Fig. 7 Light interception of maize, peanut and total in monocropping and intercropping systems at three maize densities. M represents monocropped maize; P represents monocropped peanut. Error bars are the standard error values.

Table 2 Light use efficiency (LUE) of maize and peanut in different systems, monocropping and two intercropping (M4P4 and M2P4) systems

Year	System	Maize plant density (plants m ⁻¹)	Dry matter (g·m ⁻²)		LUE (g·MJ ⁻¹ ·m ⁻²)		
			Maize	Peanut	Maize	Peanut	
2016	Monocropped peanut	–		860		1.16	
	Monocropped maize	3.0	2292 b		2.82 a		
		4.5	2961 ab		3.36 a		
		6.0	3092 a		3.39 a		
	M4P4	3.0	1347 a	382 a	2.69 a	1.44 a	
		4.5	1520 a	334 a	2.75 a	1.37 a	
		6.0	1646 a	324 a	2.80 a	1.43 a	
	M2P4	3.0	1037 b	481 a	2.67 b	1.28 a	
		4.5	1377 a	468 a	3.07 ab	1.29 a	
		6.0	1505 a	409 a	3.18 a	1.23 a	
	2017	Monocropped peanut	–		1003		1.36
		Monocropped maize	3.0	1932 b		2.53 b	
4.5			2520 a		3.06 a		
6.0			2472 a		2.83 ab		
M4P4		3.0	1282 b	402 a	2.80 a	1.45 a	
		4.5	1609 a	344 a	3.07 a	1.32 a	
		6.0	1608 a	335 a	2.95 a	1.39 a	
M2P4		3.0	963 b	518 a	2.61 a	1.37 a	
		4.5	1246 a	478 a	2.98 a	1.39 a	
		6.0	1233 a	471 a	2.71 a	1.46 a	
Interaction			<i>P</i> value				
Density			0.000	0.001	0.002	0.801	
System			0.000	0.000	0.177	0.032	
Year			0.001	0.035	0.073	0.118	
Density × System			0.108	0.921	0.367	0.525	
Density × Year			0.327	0.814	0.225	0.588	
System × Year			0.008	0.384	0.007	0.019	
Density × System × Year			0.698	0.576	0.550	0.255	

Note: Means followed by same letter indicate no significantly different between densities in a certain system at $\alpha = 0.05$ level. M4P4 is intercropping of four rows maize with four rows peanut; M2P4 is intercropping of two rows maize with four rows of peanut.

area index in the intercropping system was not greatly affected, resulting in a relatively stable level of light interception.

Intercropping did not affect maize LUE but increased peanut LUE. The LUE of component crops varies between studies. Most studies report that tall C₄ cereal species in intercropping had similar LUE in intercrops and monocrops^[14,40], but yield increased with increased light interception. However, although the shorter intercropped peanut intercepted much less light than monocropped peanut, it had an increased LUE as a result of the

lower ratio of direct to diffuse light under the shading by maize^[25,42]. The higher LUE of peanut in intercropping contributed to production of more biomass per unit of light, compensating the negative light interception under shading.

Plant density affects crop LUE^[43]. Here, the LUE of intercropped maize increased with increasing maize plant density. The LUE of maize may be closely related to differences in morphological traits^[44] from intraspecific competition due to increasing density, especially in border rows^[16,45]. More later season

growth with an increased number of green leaves in the canopy^[44] and delayed leaf senescence^[46] at higher plant density can also result in an increase in LUE. However, our study did not reveal more later season growth. Future studies are needed to explore the leaf senescence of intercropped maize. The LUE with greater shading might be expected to be higher.

Plant density affects the performance of crops, for example the specific leaf area increases with increasing density^[47], with plants growing taller at high plant density than at low plant density^[26]. Here, we found that the plant height of intercropped maize was not affected by plant density but was affected in the monocropping system (Fig. 2). Crop lodging is a common phenomenon in maize production in north China due to climate change, especially with more frequent extreme weather events^[48,49]. Xu et al.^[50] reported that the maize lodging rate was positively correlated with plant height. Intercropping might therefore help to reduce the risk of lodging and this can be examined in future studies.

5 CONCLUSIONS

Light interception in maize-peanut intercropping at system level was higher than in monocropped peanut but lower than in monocropped maize. Despite similar LUE in monocropped and intercropped maize, peanut with shading used light more efficiently. The density effect on light interception of intercropped maize was smaller than that in monocropping. This provides further evidence for a lower optimum plant density of dominant species in intercropping than in monocropping as previously reported^[33]. Row configurations (strip width) might affect light interception and LUE of intercropping although there was no evident difference between M2P4 and M4P4 intercrops. It would be interesting to explore additional strip widths in future studies in relation to differences in environment, management and genotypes. Our results help in understanding the mechanisms of intra- and interspecific competition in intercropping and in system design optimization for sustainable agriculture.

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Compliance with ethics guidelines

Qi Wang, Zhanxiang Sun, Wei Bai, Dongsheng Zhang, Yue Zhang, Ruonan Wang, Wopke van der Werf, Jochem B. Evers, Tjeerd-Jan Stomph, Jianping Guo, and Lizhen Zhang declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

REFERENCES

- Martin-Guay M O, Paquette A, Dupras J, Rivest D. The new Green Revolution: sustainable intensification of agriculture by intercropping. *Science of the Total Environment*, 2018, **615**: 767–772
- Meng Q F, Sun Q P, Chen X P, Cui Z L, Yue S C, Zhang F S, Romheld V. Alternative cropping systems for sustainable water and nitrogen use in the North China Plain. *Agriculture, Ecosystems & Environment*, 2012, **146**(1): 93–102
- Yu Y, Stomph T J, Makowski D, van der Werf W. Temporal niche differentiation increases the land equivalent ratio of annual intercrops: a meta-analysis. *Field Crops Research*, 2015, **184**: 133–144
- Zhang L, van der Werf W, Bastiaans L, Zhang S, Li B, Spiertz J H J. Light interception and radiation use efficiency in relay intercrops of wheat and cotton. *Field Crops Research*, 2008, **107**(1): 29–42
- Mao L L, Zhang L, Li W Q, van der Werf W, Sun J H, Spiertz H, Li L. Yield advantage and water saving in maize/pea intercrop. *Field Crops Research*, 2012, **138**: 11–20
- Li L, Zhang L Z, Zhang F S. Crop mixtures and the mechanisms of overyielding. *Encyclopedia of Biodiversity (second edition)*, 2013: 382–395
- Boudreau M A. Diseases in intercropping systems. *Annual Review of Phytopathology*, 2013, **51**(1): 499–519
- Liebman M, Dyck E. Crop rotation and intercropping strategies for weed management. *Ecological Applications*, 1993, **3**(1): 92–122
- Risch S J. Intercropping as cultural pest control: Prospects and limitations. *Environmental Management*, 1983, **7**(1): 9–14
- Cai Q, Zhang Y, Sun Z, Zheng J, Bai W, Zhang Y, Liu Y, Feng L, Feng C, Zhang Z, Yang N, Evers J B, Zhang L. Morphological plasticity of root growth under mild water stress increases water

- use efficiency without reducing yield in maize. *Biogeosciences*, 2017, **14**(16): 3851–3858
11. Maddonni G A, Chelle M, Drouet J L, Andrieu B. Light interception of contrasting azimuth canopies under square and rectangular plant spatial distributions: simulations and crop measurements. *Field Crops Research*, 2001, **70**(1): 1–13
 12. Maddonni G A, Otegui M E, Cirilo A G. Plant population density, row spacing and hybrid effects on maize canopy architecture and light attenuation. *Field Crops Research*, 2001, **71**(3): 183–193
 13. Lizaso J I, Batchelor W D, Westgate M E, Echarte L. Enhancing the ability CERES-Maize to compute light capture. *Agricultural Systems*, 2003, **76**(1): 293–311
 14. Gao Y, Duan A, Qiu X, Sun J, Zhang J, Liu H, Wang H. Distribution and use efficiency of photosynthetically active radiation in strip intercropping of maize and soybean. *Agronomy Journal*, 2010, **102**(4): 1149–1157
 15. Keating B A, Carberry P S. Resource capture and use in intercropping: solar radiation. *Field Crops Research*, 1993, **34**(3–4): 273–301
 16. Zhang D, Sun Z, Feng L, Bai W, Yang N, Zhang Z, Du G, Feng C, Cai Q, Wang Q, Zhang Y, Wang R, Arshad A, Hao X, Sun M, Gao Z, Zhang L. Maize plant density affects yield, growth and source-sink relationship of crops in maize/peanut intercropping. *Field Crops Research*, 2020, **257**: 107926
 17. Reynolds P E, Simpson J A, Thevathasan N V, Gordon A M. Effects of tree competition on corn and soybean photosynthesis, growth, and yield in a temperate tree-based agroforestry intercropping system in southern Ontario, Canada. *Ecological Engineering*, 2007, **29**(4): 362–371
 18. Harris D, Natarajan M, Willey R W. Physiological basis for yield advantage in a sorghum/groundnut intercrop exposed to drought. 1. Dry-matter production, yield, and light interception. *Field Crops Research*, 1987, **17**(3–4): 259–272
 19. Van Roekel R J, Coulter J A. Agronomic responses of corn to planting date and plant density. *Agronomy Journal*, 2011, **103**(5): 1414–1422
 20. Ofori F, Stem W R. Relative sowing time and density of component crops in a maize/cowpea intercrop system. *Experimental Agriculture*, 1987, **23**(1): 41–52
 21. Zhang W, Liu G, Sun J, Zhang L, Weiner J, Li L. Growth trajectories and interspecific competitive dynamics in wheat/maize and barley/maize intercropping. *Plant and Soil*, 2015, **379**(1–2): 227–238
 22. Watiki J M, Fukai S, Banda J A, Keating B A. Radiation interception and growth of maize/cowpea intercrop as affected by maize plant density and cowpea cultivar. *Field Crops Research*, 1993, **35**(2): 123–133
 23. Prasad R B, Brook R M. Effect of varying maize densities on intercropped maize and soybean in Nepal. *Experimental Agriculture*, 2005, **41**(3): 365–382
 24. Hammer G L, Wright G C. A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. *Australian Journal of Agricultural Research*, 1994, **45**(3): 575–589
 25. Sinclair T R, Muchow R C. Radiation use efficiency. *Advances in Agronomy*, 1999, **65**: 215–265
 26. Zhang D, Zhang L, Liu J, Han S, Wang Q, Evers J, Liu J, van der Werf W, Li L. Plant density affects light interception and yield in cotton grown as companion crop in young jujube plantations. *Field Crops Research*, 2014, **169**: 132–139
 27. Liu X, Rahman T, Song C, Yang F, Su B, Cui L, Bu W, Yang W. Relationships among light distribution, radiation use efficiency and land equivalent ratio in maize-soybean strip intercropping. *Field Crops Research*, 2018, **224**: 91–101
 28. Borrás L, Maddonni G A, Otegui M E. Leaf senescence in maize hybrids: plant population: row spacing and kernel set effects. *Field Crops Research*, 2003, **82**(1): 13–26
 29. Jia Q, Sun L, Mou H, Ali S, Liu D, Zhang Y, Zhang P, Ren X, Jia Z. Effects of planting patterns and sowing densities on grain-filling, radiation use efficiency and yield of maize (*Zea mays* L.) in semi-arid regions. *Agricultural Water Management*, 2018, **201**: 287–298
 30. Wang Q, Zhang D, Zhang L, Han S, van der Werf W, Evers J B, Su Z, Anten N P R. Spatial configuration drives complementary capture of light of the understory cotton in young jujube plantations. *Field Crops Research*, 2017, **213**: 21–28
 31. Peel M C, Finlayson B L, McMahon T A. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences Discussions*, 2007, **4**: 439–473
 32. Food and Agriculture Organization of the United Nations (FAO). World Reference Base for Soil Resources 2014: International Soil Classification System for Naming Soils and Creating Legends for Soil Maps. Rome: FAO, 2015. Available at FAO website on March 13, 2021
 33. Wang Q, Bai W, Sun Z, Zhang D, Zhang Y, Wang R, Evers J B, Stomph T, van der Werf W, Feng C, Zhang L. Does reduced intraspecific competition of the dominant species in intercrops allow for a higher population density? *Food and Energy Security*, 2021, **10**(2): 285–298
 34. Yin X, Goudriaan J, Lantinga E A, Vos J, Spiertz H J. A flexible sigmoid function of determinate growth. *Annals of Botany*, 2003, **91**(3): 361–371
 35. Gou F, van Ittersum M K, Simon E, Leffelaar P A, van der Putten P E L, Zhang L, van der Werf W. Intercropping wheat and maize increases total radiation interception and wheat RUE but lowers maize RUE. *European Journal of Agronomy*, 2017, **84**: 125–139
 36. Sivakumar M V K, Virmani S M. Crop productivity in relation to interception of photosynthetically active radiation. *Agricultural and Forest Meteorology*, 1984, **31**(2): 131–141
 37. Collino D J, Dardanelli J L, Sereno R, Racca R W. Physiological responses of argentine peanut varieties to water stress: light interception, radiation use efficiency and partitioning of assimilates. *Field Crops Research*, 2001, **70**(3): 177–184
 38. Davidian M, Giltinan D M. Nonlinear mixed effects models for repeated measurement data: an overview and update. *Journal of Agricultural Biological & Environmental Statistics*, 2003, **8**(4): 387–419
 39. Bolker B. Likelihood and all that. In: Bolker B, eds. *Ecological*

- models and data in R. Princeton University Press, Princeton and Oxford, 2007, 228–234
40. Awal M A, Koshi H, Ikeda T. Radiation interception and use by maize/peanut intercrop canopy. *Agricultural and Forest Meteorology*, 2006, **139**(1–2): 74–83
 41. Maddonni G A, Otegui M E. Leaf area, light interception, and crop development in maize. *Field Crops Research*, 1996, **48**(1): 81–87
 42. Healey K D, Hammer G L, Rickert K G, Bange M P. Radiation use efficiency increases when the diffuse component of incident radiation is enhanced under shade. *Australian Journal of Agricultural Research*, 1998, **49**(4): 665–672
 43. Worku W, Demisie W. Growth, light interception and radiation use efficiency response of pigeon pea (*Cajanus cajan*) to planting density in southern Ethiopia. *Journal of Agronomy*, 2012, **11**(4): 85–93
 44. Mao L, Zhang L, Zhao X, Liu S, van der Werf W, Zhang S, Spiertz H, Li Z. Crop growth: light utilization and yield of relay intercropped cotton as affected by plant density and a plant growth regulator. *Field Crops Research*, 2014, **155**: 67–76
 45. Wang R, Sun Z, Zhang L, Yang N, Feng L, Bai W, Zhang D, Wang Q, Evers J B, Liu Y, Ren J, Zhang Y, van der Werf W. Border-row proportion determines strength of interspecific interactions and crop yields in maize/peanut strip intercropping. *Field Crops Research*, 2020, **253**: 107819
 46. Dong H, Li W, Eneji A E, Zhang D. Nitrogen rate and plant density effects on yield and late-season leaf senescence of cotton raised on a saline field. *Field Crops Research*, 2012, **126**: 137–144
 47. Yao H, Zhang Y, Yi X, Zhang X, Zhang W. Cotton responds to different plant population densities by adjusting specific leaf area to optimize canopy photosynthetic use efficiency of light and nitrogen. *Field Crops Research*, 2016, **188**: 10–16
 48. Xue J, Dong P F, Hu S P, Li L L, Wang K R, Gao S, Wang Y Z, Li S K. Effect of lodging on maize grain loss and loss reduction technology in mechanical grain harvest. *Maize Sciences*, 2020, **28**(6): 116–120 (in Chinese)
 49. Gong L, Qu S, Huang G, Guo Y, Zhang M, Li Z, Zhou Y, Duan L. Improving maize grain yield by formulating plant growth regulator strategies in North China. *Journal of Integrative Agriculture*, 2021, **20**(2): 622–632
 50. Xu C, Gao Y, Tian B, Ren J, Meng Q, Wang P. Effects of ED4H, a novel plant growth regulator, on mechanical strength, stalk vascular bundles and grain yield of summer maize at high densities. *Field Crops Research*, 2017, **200**: 71–79